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THE RESPIRATION OF POTATO TUBERS IN RELATION TO THE OCCURRENCE OF BLACKHEART

BY

J. P. BENNETT AND E. T. BARTHOLOMEW

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INTRODUCTION

The artificial production of blackheart in potato tubers was accomplished by Bartholomew[3] in 1915. He found that exposing potatoes to temperatures of 38° to 48° C. with free access of air, for 15 to 20 hours resulted in the subsequent blackening of the interior regions of the tuber after removal to ordinary temperatures. Most marked results were obtained by exposure between 42° and 44° C., and this range was at that time designated as the optimum temperature for the production of this pathological condition.

Bartholomew ascribed the production of the injury to a deficiency of oxygen in the injured regions of the tuber, brought about as a result of the increased rate of respiration of the tissues. Under these conditions the available supply of oxygen diffusing inward from the surface of the tuber was used up before it reached the interior tissues which died as a result of asphyxiation. When oxygen was allowed to penetrate to these tissues later, they blackened in consequence of the action of tyrosinase upon the tyrosin which is normally present in the uninjured tuber and in increased amount in the injured regions.

That the oxygen supply was of first importance to the production of blackheart in heated tubers was confirmed by other experiments of Bartholomew in which the external supply of oxygen was varied, or its penetration into the interior tissues of the tuber favored. It was found

that passing a stream of approximately 94% oxygen over the tubers during the period of heating prevented the development of blackheart. On the other hand, passing a stream of approximately 94% carbon dioxide over the tubers markedly increased the severity of the injury. Passing a stream of ordinary air over the tubers during the period of heating had little effect in comparison with tubers heated in still air. It was learned subsequently that partly or completely peeling the tubers, or abrading their surfaces by hacking with a knife usually lessened or prevented injury. The time of heating required to produce blackheart in tubers thus treated was longer than when the skin was left intact, the injury was less severe or did not occur within the usual period of heating. It was also noticed that large tubers were more susceptible to injury than small ones.

At the time Bartholomew published his results he did not suspect that blackheart could be produced at temperatures lower than 38° C., although oxygen supply was shown to be the prime factor in its production. It was shown by Stewart and Mix[15] in 1917 that blackheart could be produced readily at low temperatures by restricting the supply of oxygen sufficiently. Using jars and tanks entirely or partly filled with tubers, sealed air-tight and placed at various temperatures ranging from 2° to 24° C., for periods ranging from a few days to 58 days, they were able to produce typical blackheart. With partly filled containers, or lower temperatures, longer exposure was required to produce the injury than with filled containers or higher temperatures. With a volume of air equal to that of the tubers in the containers an exposure of 10–12 days at about 21° C., of about 20 days at 12°–16° C., and of 23–40 days at about 5° C., was required to produce blackheart. With a larger proportion of air to tubers a longer exposure was required. When the ratio of volume of air to volume of tubers was 26.9 or greater no blackheart was produced in 40 days at a temperature of 15°–22° C.

It was further shown by Stewart and Mix that deficient oxygen supply and not the accumulation of carbon dioxide resulting from the respiration processes was directly responsible for the injury. In experiments with tubers in sealed containers, into some of which were placed solutions of sodium hydroxide sufficient to absorb the carbon dioxide produced, blackheart occurred about equally severely in all jars.

Mann and Joshi,[9] in India, found that tubers heated in open wire baskets in ordinary air at a temperature of 27°–30° C., remained sound for periods longer than twelve days. When heated at 36° C., under the same conditions of aeration, blackheart occured in about six days. At 41°–42° C., the injury was very marked in two days. When the tubers were placed in sealed containers in which the air was replaced by carbon dioxide or nitrogen, or when the tubers were coated with collodion or paraffin, blackheart was found to develop at 27°–30° C., in six to twelve days. At 36° C., injury had occurred on the third day. These results are in agreement with the observations of Bartholomew, except that he did not find the occurrence of blackheart at a temperature lower than 38° C. Tubers exposed by Bartholomew at 32°–33° C., were uninjured after 16 days. These tubers, however, were placed in the oven only at night and left at laboratory temperatures during the day. Exposure for two successive nights at 38°–39° C., with removal to laboratory temperatures during the day, resulted in the appearance of blackheart in some of the tubers. Later observations by the writers showed that continuous heating occasionally produced blackheart at temperatures as low as 25° C.

It is evident from the work of these investigators that there is a relationship between temperature, oxygen supply, and period of exposure in the production of blackheart both at the low and high ranges of temperature used. Increased temperature and reduced supply of oxygen apparently decrease the period of exposure required to induce blackheart.

The gaseous exchange between the tubers and the surrounding atmosphere has not previously been followed, and the conditions obtaining at the time when injury appears are inadequately known, except in those cases where blackheart has been produced by heating the tubers in normal air. It is the purpose of this paper to report a more extended study of the relationship of temperature, time, and oxygen supply in the production of blackheart. Such a study appears desirable, since blackheart has been reported to occur not only during shipment in heated cars, but during storage, and in the field, especially in the western states. Its occurrence in the field has been reported from six counties in interior valleys of central and southern California. Its occurrence in the field in Utah has been reported to one of the writers by Dr. B. L. Richards of the Utah Experiment Station, and in Idaho

by Dr. G. K. K. Link of the U. S. Dept. of Agriculture. A reputed case of considerable loss due to blackheart in cold storage was brought to the writers' attention in San Francisco in 1920.*

Methods

Measured volumes of tubers were sealed in containers of known capacity so as to provide a definite ratio of air volume to volume of tubers. Each series, consisting of five to eleven containers, was then held at a uniform temperature. At successive intervals one or more containers were removed, samples of the atmosphere withdrawn and analyzed. The containers were then opened and the condition of the tubers observed. Each series was kept at a given temperature until blackheart appeared in the tubers removed at two or more successive times.

The containers used were glass jars of approximately 5½ liters capacity, with ground lids pierced by two holes closed with glass stopcocks. To the inner end of one stopcock was attached a rubber tube which extended to the bottom of the jar. The tubers were supported near the middle of the jar on an inverted wire basket. The sealed jars were tested for air-tightness by introducing compressed air and immersing in water. After placing the jars in the incubator or cold storage room the stopcocks were left open, or opened at frequent intervals, until the jars and contents had reached the temperature of their surroundings. The stopcocks were then closed and remained so until removal of the jar. On removing each jar any change of pressure of the atmosphere within was determined by means of a manometer. The atmosphere within the jar was then thoroughly mixed by agitation, and two samples withdrawn, one from the upper and the other from the lower part of the jar. Before opening, the jar was again tested for air-tightness.

* The work reported here was begun in 1918 at the University of Wisconsin for the U. S. Dept. of Agriculture, Bureau of Plant Industry. Since 1919 the work has been carried on at the University of California at Berkeley. Acknowledgment is due to the Botany Department of the University of Wisconsin for certain facilities, to the Office of Cotton, Truck, and Forage Crop Disease Investigations, U. S. Dept. of Agriculture for support during the early part of the work and to the Division of Agronomy, College of Agriculture, for the tubers used in the work at Berkeley.

The duplicate gas samples were analyzed for oxygen and carbon dioxide over mercury by means of a Hempel or an Orsat apparatus, readings being made to two-tenths of one per cent. The results of analyses are in all cases expressed as per cent of volume.

The tubers used in the work at Wisconsin were of the varieties Rural New Yorker and Green Mountain Jr., obtained from a local seedsman and stored in a cellar at a temperature of 10°–15° C. previous to use. The experiments were begun in November so that the tubers which were locally grown were past or very nearly past their normal rest period when first used. The tubers used in the work at Berkeley were of the variety Netted Gem, grown in Nevada, purchased on the local market in October, and stored at 5° C. until used. Experiments were begun in December so that these tubers were also past their normal rest period at the time of use. The volumes of potatoes placed in the jars were calculated from their specific gravity which was found to average approximately 1.1. The ratio of volume of air to volume of tubers in each jar varied in the work in Wisconsin, from 5.8 to 7.0; in the work at Berkeley the ratio was approximately 6. The tubers were weighed to within 5 grams of the calculated required weight. The number of tubers in each jar varied from 5 to 7 in all but a few instances.

The intervals between removals of jars in a given series varied from one hour at the highest temperature to one week at the lowest temperature. On removal of the tubers after exposure they were split longitudinally and exposed to the laboratory air for several hours before observations were made. In recording the condition of the tubers three stages of severity of injury were recognized: "slight," denoting small injured areas of less than one-tenth the area of the exposed cut surface of the tuber; "moderate," indicating an injured area amounting to between one-tenth and one-third of the cut surface; and "severe," applying to those showing still greater extent of injury. No attempt was made to determine the actual volume of tissue injured, but on the basis just noted it would correspond roughly to less than 0.1 per cent of the tuber volume for slight, 0.1 to 4 per cent for moderate, and over 4 per cent for severe injury. In each series the end of the period required for the development of blackheart was determined by the first jar in which blackheart appeared in one or more tubers when

followed by its appearance in the succeeding withdrawals. The series usually extended beyond this point, acting thus as a check upon the first observations.

The incubators and cold storage rooms utilized in these experiments were automatically regulated to within 1° C. The experiments were conducted at temperatures ranging from 0° to 45° C., the intervals being two and a half degrees between 0° and 10° C., and five degrees between 10° and 45° C.

Data

Table 1 presents the data obtained in Wisconsin with Rural New Yorker and Green Mountain Jr. potatoes. Control experiments were conducted in parallel with those in sealed jars, with an equal number of tubers from the same lot placed in wire baskets.

In table 1, and in all succeeding tables, all values in horizontal columns referring to gas content of jars are expressed as per cent of volume. Since the ratio of volume of gas to volume of tubers was approximately the same in all jars, the values for the content of carbon dioxide and oxygen in the different jars may be compared directly. No marked changes in pressure of the gases in the jars occurred in these experiments. In the horizontal columns referring to the condition of tubers the sum of the numbers in each section indicates the total number of tubers in the jar opened at that point of the series. The signs refer to presence or absence of blackheart as follows: — indicates that no blackheart had developed; + indicates slight; ++ moderate; and +++ severe injury with corresponding development of blackheart, as described for these designations in the preceding section of this paper.

TABLE 1

GASEOUS EXCHANGE AND THE PRODUCTION OF BLACKHEART IN RURAL NEW YORKER AND GREEN MOUNTAIN JR. POTATO TUBERS WHEN SUBJECTED TO DIFFERENT TEMPERATURES IN SEALED CHAMBERS

	Rural New Yorker tubers							Green Mountain Jr. tubers						
Temperature	40° C.							40° C.						
Time, days	0	1/6	1/3	1/2	1			0	1/6	1/3	1/2	1		
CO_2 evolved %	0	1.2	3.4	5.4	9.2			0	1.6	4.2	6.6	11.2		
O_2 remaining %	21	19.8	17.4	15.2	11.6			21	19.2	16.6	14.2	9.2		
CO_2+O_2 present %	21	21.0	20.8	20.6	20.8			21	20.8	20.8	20.8	20.4		
Ratio CO_2 evolved to O_2 absorbed		1.0	0.94	0.95	0.98				0.89	0.95	0.97	0.95		
Blackheart in tubers in jars	6−	5−	6+	1+				6−	4−	1−	2++			
		1+		4++					2+	3+	4+++			
				1+++						2++				
Blackheart in control tubers	6−	5−	4−	1−				6−	6−	3−	1+			
		1+	2+	4++						3+	3++			
				1+++							2+++			
Temperature	35° C.							35° C.						
Time, days	0	1/3	2/3	1	1 1/3			0	1/3	2/3	1	1 1/3		
CO_2 evolved %	0	2.2	4.8	7.6	9.6			0	2.6	6.0	9.6	12.2		
O_2 remaining %	21	18.4	15.8	13.0	10.4			21	18.2	14.2	10.4	7.2		
CO_2+O_2 present %	21	20.6	20.6	20.6	20.0			21	20.8	20.2	20.0	19.4		
Ratio CO_2 evolved to O_2 absorbed		0.85	0.92	0.95	0.91				0.93	0.88	0.91	0.88		
Blackheart in tubers in jars		6−	5−	5−	6+				8−	3−	3−	2−		
			1+	1+					1+	4+	3+	4++		
											3++	4+++		
Blackheart in control tubers		6−	6−	6−	4−				9−	4−	4−	3−		
					2+					3+	5+	5+		
												2++		

TABLE 1—(*Continued*)

	Rural New Yorker tubers							Green Mountain Jr. tubers						
Temperature	30° C.							30° C.						
Time, days	0	1	2	3	4			0	1	2	3	4		
CO_2 evolved %	0	6.4	10.4	14.2	18.0			0	7.8	12.4	16.6	22.4		
O_2 remaining %	21	14.2	9.2	5.8	2.0			21	13.0	7.8	3.2	0.4		
CO_2+O_2 present %	21	20.6	19.6	20.0	20.0			21	20.8	20.2	19.8	22.8		
Ratio CO_2 evolved to O_2 absorbed		0.94	0.83	0.93	0.95				0.97	0.94	0.93	1.09		
Blackheart in tubers in jars		6−	5−	3− 2+	2+ 4++				5− 1+	3− 3+	1+ 3++ 2+++	6+++		
Blackheart in control tubers		6−	5−	5−	6−				6−	5− 1+	6−	4− 2+		
Temperature	25° C.							25° C.						
Time, days	0	1	2	3	4	5	6	0	1	2	3	4	5	6
CO_2 evolved %	0	4.6	8.0	10.8	12.4	14.8	16.6	0	6.4	10.6	14.0	16.8	19.2	20.0
O_2 remaining %	21	15.6	12.2	8.8	6.6	4.2	2.8	21	14.4	9.8	6.0	3.0	1.2	0.8
CO_2+O_2 present %	21	20.2	20.2	19.6	19.0	19.0	19.4	21	20.8	20.4	20.0	19.8	19.4	20.8
Ratio CO_2 evolved to O_2 absorbed		0.85	0.91	0.89	0.86	0.83	0.91		0.97	0.95	0.93	0.93	0.92	0.98
Blackheart in tubers in jars		7−	7−	7−	7−	6− 1+	2− 4++		6−	6−	6−	5− 1+	4− 2+	2− 4+
Blackheart in control tubers		7−	7−	7−	7−	7−	7−		6−	6−	6−	6−	6−	4− 2+

TABLE 1—(*Concluded*)

	Rural New Yorker tubers							Green Mountain Jr. tubers						
Temperature	20° C.							20° C.						
Time, days	0	1	3	5	7	9	11	0	1	3	5	7	9	11
CO_2 evolved %	0	2.6	7.4	10.2	13.2	15.2	17.2	0	3.4	10.4	13.2	15.6	21.0	23.4
O_2 remaining %	21	18.2	11.4	8.4	4.6	2.8	1.4	21	17.6	9.8	7.0	4.0	1.0	0
CO_2+O_2 present %	21	20.8	18.8	18.6	17.8	18.0	18.6	21	21.0	20.2	20.2	19.6	22.0	23.4
Ratio CO_2 evolved to O_2 absorbed		0.93	0.77	0.81	0.81	0.84	0.88		1.0	0.93	0.94	0.92	1.05	1.11
Blackheart in tubers in jars		7−	7−	7−	7−	6−	2−		8−	8−	7−	7−	6−	2−
						1+	5+						1+	4+
														1++
Blackheart in control tubers		7−	7−	7−	7−	7−	7−		8−	8−	7−	7−	7−	7−

TABLE 2

GASEOUS EXCHANGE AND THE PRODUCTION OF BLACKHEART IN NETTED GEM POTATO TUBERS WHEN SUBJECTED TO DIFFERENT TEMPERATURES IN SEALED CHAMBERS

Temperature	45° C.										
Time, days	0	2/24	3/24	4/24	5/24	6/24	8/24				
CO_2 evolved %	0	1.8	2.4	3.6	4.8	5.2	5.2				
O_2 remaining %	21	18.2	18.0	16.6	15.4	15.0	14.6				
CO_2+O_2 present %	21	20.0	20.4	20.2	20.2	20.2	19.8				
Ratio CO_2 evolved to O_2 absorbed		0.63	0.80	0.82	0.86	0.87	0.81				
Blackheart in tubers		5−	5−	3− 2+	4− 1+	4− 1++	1− 4++				
Temperature	40° C.										
Time, days	0	4/24	6/24	7/24	8/24	9/24	10/24	12/24	18.5/24	1	1½
CO_2 evolved %	0	2.8	4.4	5.0	6.0	6.8	7.0	7.8	12.2	15.0	21.6
O_2 remaining %	21	17.2	15.6	15.2	14.2	12.8	13.2	12.2	9.2	7.2	2.8
CO_2+O_2 present %	21	20.0	20.0	20.2	20.2	19.6	20.2	20.0	21.4	22.2	24.4
Ratio CO_2 evolved to O_2 absorbed		0.74	0.81	0.86	0.88	0.83	0.90	0.89	1.13	1.09	1.18
Blackheart in tubers		5−	5−	3− 3+	2− 3+ 2++	1− 4++	2+ 3++	1+ 4++	3++ 3+++	1+ 4+++	5+++

TABLE 2—(*Continued*)

Temperature	35° C.										
Time, days	0	2	3	3½	4	5					
CO_2 evolved %	0	13.0	15.8	20.0	24.8	25.4					
O_2 remaining %	21	5.0	3.0	1.0	0.4	0					
CO_2+O_2 present %	21	18.0	18.8	21.0	25.2	25.4					
Ratio CO_2 evolved to O_2 absorbed		0.81	0.88	1.0	1.2	1.2					
Blackheart in tubers		5−	4− 1+	3− 1+	1+ 3+++	1+ 3+++					

Temperature	30° C.										
Time, days	0	0.5	1	1.5	2	2.5	3	4	5	5.5	6
CO_2 evolved %	0	2.0	6.0	8.0	10.2	12.6	13.0	16.6	20.0	21.0	22.2
O_2 remaining %	21	17.4	13.4	11.2	8.8	6.4	5.8	2.2	0	0	0
CO_2+O_2 present %	21	19.4	19.4	19.2	19.0	19.0	18.8	18.8	20.0	21.0	22.2
Ratio CO_2 evolved to O_2 absorbed		0.56	0.79	0.82	0.84	0.86	0.86	0.88	0.95	1.00	1.06
Blackheart in tubers		5−	5−	4−	5−	5−	5−	5−	4− 1+	2− 3+	1− 3+ 1++

TABLE 2—(*Continued*)

Temperature	25° C.										
Time, days	0	1	2	3	4	5	6	7	8	9	
CO_2 evolved %	0	4.4	9.4	11.8	15.2	15.4	18.4	20.4	21.0	23.0	
O_2 remaining %	21	14.8	10.0	7.0	3.6	3.2	0.8	0	0	0	
CO_2+O_2 present %	21	19.2	19.4	18.8	18.8	18.6	19.2	20.4	21.0	23.0	
Ratio CO_2 evolved to O_2 absorbed		0.71	0.85	0.84	0.87	0.86	0.91	0.97	1.00	1.10	
Blackheart in tubers		5−	5−	5−	5−	5−	5−	2− 3+	3+ 2++	3+ 2++	
Temperature	20° C.										
Time, days	0	2	4	6	8	10	12	13			
CO_2 evolved %	0	7.0	11.8	15.4	16.2	20.4	23.4	21.4			
O_2 remaining %	21	10.8	6.0	2.0	1.4	0	0	0			
CO_2+O_2 present %	21	17.8	17.8	17.4	17.6	20.4	23.4	21.4			
Ratio CO_2 evolved to O_2 absorbed		0.69	0.79	0.81	0.83	0.97	1.11	1.02			
Blackheart in tubers		5−	5−	5−	5−	5−	3− 2+	5+			

TABLE 2—(*Continued*)

Temperature	15° C.										
Time, days	0	2	6	10	14	18	22	26	30	34	38
CO_2 evolved %	0	2.8	8.8	10.8	13.8	15.0	18.0	22.0	20.8	30.8	28.6
O_2 remaining %	21	16.0	9.2	5.6	3.4	2.0	0	0	0	0	0
CO_2+O_2 present %	21	18.8	18.0	16.4	17.2	17.0	18.0	22.0	20.8	30.8	28.6
Ratio CO_2 evolved to O_2 absorbed		0.56	0.75	0.70	0.78	0.79	0.86	1.05	0.99	1.47	1.36
Blackheart in tubers		6−	5−	5−	5−	5−	5−	5−	5−	5+	2− 3+
Temperature	10° C.										
Time, days	0	7	14	21	28	33	38	42	46	50	
CO_2 evolved %	0	7.6	15.4	20.8	21.4	24.6	22.8	25.6	28.2	30.0	
O_2 remaining %	21	10.4	1.8	0	0	0	0	0	0	0	
CO_2+O_2 present %	21	18.0	17.2	20.8	21.4	24.6	22.8	25.6	28.2	30.0	
Ratio CO_2 evolved to O_2 absorbed		0.72	0.80	0.99	1.02	1.17	1.08	1.22	1.34	1.43	
Blackheart in tubers		6−	6−	7−	6−	5−	5−	2− 3+	3+ 2++	4++ 1+++	

TABLE 2—(*Continued*)

Temperature	7.5° C.											
Time, days	0	8	16	22	29	35	44	50	57	64	73	78
CO_2 evolved %	0	4.2	7.2	11.6	13.2	15.4	18.8	19.0	20.6	22.8	27.2	42.8
O_2 remaining %	21	14.0	6.4	3.4	1.0	0	0	0	0	0	0	0
CO_2+O_2 present %	21	18.2	13.6	15.0	14.2	15.4	18.8	19.0	20.6	22.8	27.2	42.8
Ratio CO_2 evolved to O_2 absorbed		0.60	0.49	0.66	0.66	0.73	0.90	0.91	0.98	1.09	1.3	2.0
Blackheart in tubers		6−	5−	5−	5−	5−	5−	4− 1++	3− 2++	1− 2+ 2++	1++ 4+++	1+ 4+++
	5° C.											
Time, days	0	7	14	21	28	35	42	49	56	70	77	84
CO_2 evolved %	0	3.8	8.2	13.0	16.8	19.8	19.2	21.6	23.2	25.0	26.4	34.2
O_2 remaining %	21	14.4	9.8	3.6	0	0	0	0	0	0	0	0
CO_2+O_2 present %	21	18.2	18.0	16.6	16.8	19.8	19.2	21.6	23.2	25.0	26.4	34.2
Ratio CO_2 evolved to O_2 absorbed		0.58	0.73	0.75	0.80	0.94	0.92	1.03	1.10	1.19	1.26	1.63
Blackheart in tubers		5−	5−	5−	5−	5−	5−	5−	5−	5+*	5++	5++

* Injury occurred on surface only; no injury appeared in interior of tubers. In two following jars injury occurred both on surface and in interior of tubers.

TABLE 2—(*Concluded*)

Temperature	2.5° C.										
Time, days	0	8	14	21	29	36	41	47	54	61	
CO_2 evolved %	0	3.2	6.4	9.6	15.4	19.0	22.4	22.8	21.4	24.8	
O_2 remaining %	21	14.0	10.0	5.0	1.0	0	0	0	0	0	
CO_2+O_2 present %	21	17.2	16.4	14.6	16.4	19.0	22.4	22.8	21.4	24.8	
Ratio CO_2 evolved to O_2 absorbed		0.46	0.58	0.60	0.77	0.90	1.07	1.09	1.02	1.18	
Blackheart in tubers		8−	5−	6−	6−	4− 2+	5−	4− 1+	4+ 2++	3++ 2+++	
Temperature	0° C.										
Time, days	0	7	15	23	30	37	40	44	47		
CO_2 evolved %	0	2.8	8.8	15.8	18.0	22.2	22.0	22.4	20.8		
O_2 remaining %	21	16.2	8.4	0.8	0	0	0	0	0		
CO_2+O_2 present %	21	19.0	17.2	16.6	18.0	22.2	22.0	22.4	20.8		
Ratio CO_2 evolved to O_2 absorbed		0.58	0.70	0.78	0.86	1.06	1.05	1.07	0.99		
Blackheart in tubers		5−	8−	8−	6−	5− 2+	7+ 1++	3+ 3++ 2+++	4++ 2+++		

The studies were not carried further in Wisconsin because of the lack of controlled temperatures below 20° C. The data presented in table 2 were obtained at Berkeley where cold storage facilities were available in addition to incubators. Since Bartholomew[3] found differences in susceptibility to blackheart among different varieties it was necessary to repeat the experiments at the higher temperatures in the work at Berkeley. Control experiments were not conducted in any case at Berkeley, dependence being placed upon the continuity of each series, adjoining jars thus serving as checks.

In table 3, is presented a summary of the data given in detail in table 2, showing the results obtained with Netted Gem tubers. The calculations of average daily absorption of oxygen (column 7) were based upon the period between the beginning of the series and the point where total exhaustion of oxygen occurred in the series. In all other cases, except where noted, the values given are based upon the single jar removed at the time when the initial appearance of blackheart occurred. This jar was the culminating point of each series and represents fairly well the average condition in the series at that point. The values in columns 1, 3, 4, 5, 6 and 9 are shown graphically in figure 1.

Columns 10, 11 and 12 show the maximum effects of the unequal rates of absorption of oxygen and evolution of carbon dioxide upon the total amounts of these two gases in the atmospheres of the jars. The values for respiratory ratios in column 13 show the relative absorption of oxygen and evolution of carbon dioxide which had occurred up to this time.

In table 4 is shown the effect upon the rate of respiration of the exhaustion of the free oxygen from the atmosphere of the jars. The values given in all instances are the averages of the results from all the jars removed previous to the time of total disappearance of oxygen (middle horizontal column), and from all the jars removed between that point and the first appearance of blackheart in the series (lower horizontal column). Where widely varying or abnormally appearing averages are given the values from which these averages were obtained are given in parentheses. The abnormally low value for the period without free oxygen at 10° C. cannot be explained with the available data.

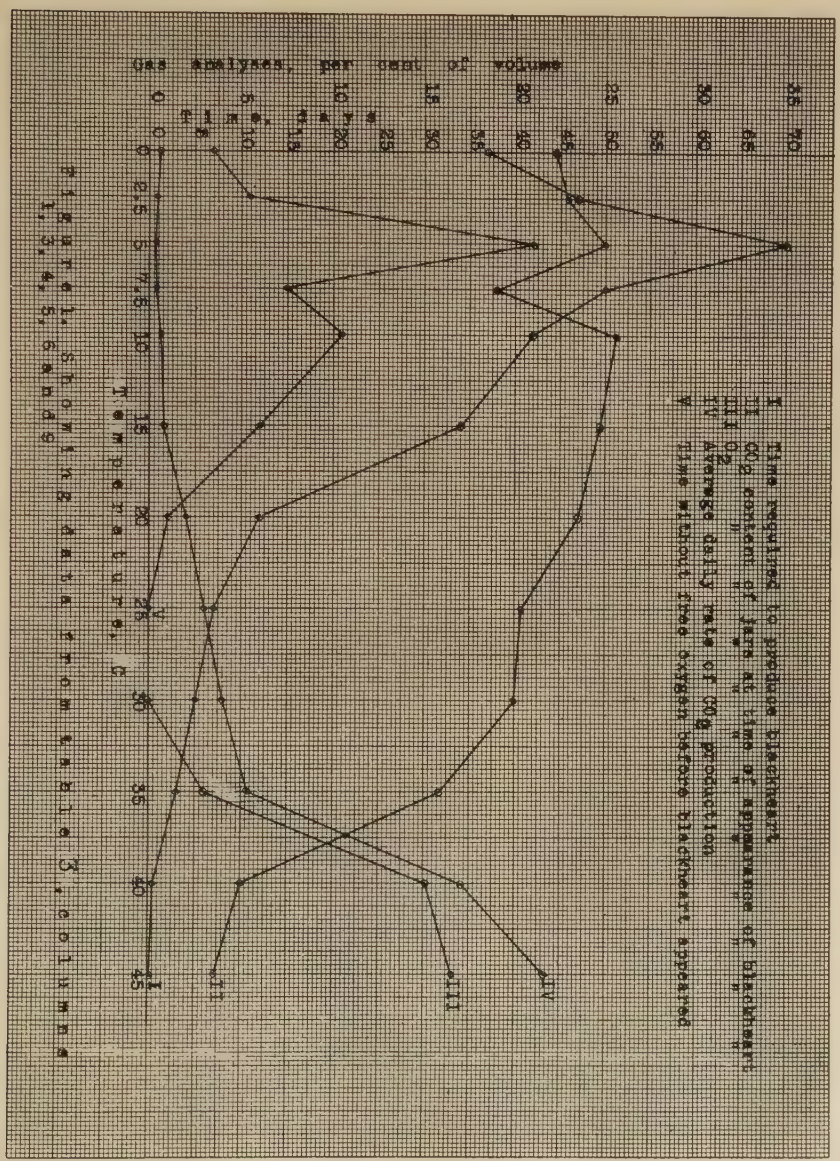
Gas analyses, per cent. of volume
Time, days
Hours of light and darkness, Eastern Standard Time
Time required to produce blackheart
CO2 content of air at time of appearance of blackheart
Average daily rate of CO2 production
Time without free oxygen before blackheart appeared
I
II
III
IV

TABLE 3

A Summary of the Main Results of Table 2

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
			Analyses of gases in jar at time blackheart appeared						CO_2+O_2 minimum in each series			Respiratory ratios		
Temperature	Interval of observations	Period of exposure to produce blackheart	CO_2	O_2	Aver. daily production of CO_2	Aver. daily absorption of O_2	Period for total absorption of O_2 in jar	Period without free O_2 before blackheart appeared	CO_2+O_2	Decrease from 21%	Time of appearance after start	At minimum of CO_2+O_2 $\frac{CO_2}{O_2}$	At total absorption of oxygen $\frac{CO_2}{O_2}$	At onset of black heart $\frac{CO_2}{O_2}$
C.	Days	Days	%	%	%	%	Days	Days	%	%	Days			
0	3 to 8	37	22.2	0	0.60	0.7	30	7	16.6	4.4	23	0.79	0.86	1.06
2.5	5 to 8	47	22.8	0	0.49	0.6	36	11	14.6	6.4	21	0.60	.90	1.08
5	7	70	25.0	0	0.36	0.7	28	42	16.6	4.4	21	0.73	.80	1.14
7.5	4 to 7	50	19.0	0	0.38	0.6	35	15	13.6	7.4	16	0.49	.73	0.91
10	5 to 9	42	25.6	0	0.6	1.0	21	21	17.2	3.8	14	0.80	.99	1.22
15	4	34	30.8	0	0.9	1.0	22	12	16.4	4.6	10	0.70	.86	1.47
			(24.7)*		(0.7)*									(1.18)*
20	2	12	23.4	0	2.00	2.1	10	2	17.4	3.6	6	0.81	.97	1.11
25	1	7	20.4	0	2.9	3.0	7	0	18.6	2.4	5	0.84	.97	0.97
30	1	5	20.0	0	4.0	4.2	5	0	18.6	2.2	3	0.86	.95	0.95
35	1	3	15.8	3.0	5.3	4.2	5	.....	18.0	3.0	2	0.81	1.21	0.88
40	1/24	7/24	5.0	15.2	17.1	19.9	.....	.....	19.6	1.4	9/24	0.81	1.19	0.86
45	1/24	4/24	3.6	16.6	21.6	26.4	.....	.....	19.8	1.2	8/24	0.81	0.81	0.82

* The values given at these points are exceptionally high. In parentheses are given values based upon the next preceding and succeeding jars, which are much more nearly representative of the series at this point.

TABLE 4

THE RATE OF PRODUCTION OF CARBON DIOXIDE BEFORE AND AFTER THE EXHAUSTION OF FREE OXYGEN FROM THE AIR IN THE CONTAINERS

Temperature C.....	20	15	10	7.5	5	2.5	0
Average daily production of carbon dioxide before exhaustion of free oxygen. %	2.62	1.10	1.03	0.48	0.59	0.48	0.58
Average daily production of carbon dioxide after exhaustion of free oxygen and before the appearance of blackheart. %	0.92	0.78	0.19 (0.09) (0.34) (0.12) (0.32)	0.27	0.25	0.35 (0.68) (0.35) (0.13)	0.43 (0.28) (0.40) (0.60)

In table 5 are shown the effects of storage for several weeks at 0° C. and 5° C. on the subsequent production of blackheart in Netted Gem tubers. After being taken out of storage, tubers from each lot were placed in an oven, having access to normal air at 40° C. One lot from each series was tested at the stated intervals in order to note the progressive development of blackheart in the two series.

TABLE 5

COMPARATIVE AMOUNTS AND SEVERITY OF BLACKHEART DEVELOPED IN NETTED GEM TUBERS, PREVIOUSLY STORED AT 0° C. AND 5° C.*

Storage temperature C.	Hours heated at 40° C.					
	21	30	42	66	90	114
0	2+ 3−	2+ 3−	3+ 2−	2+ 2++ 1+++	1+ 2+ 2+++	1+ 4+++
5	1+ 4−	1+ 4−	2+ 3−	2+ 3−	1+ 1++ 3−	2+ 2+++ 1−

* Number of tubers examined and presence and severity of blackheart indicated as in previous tables.

In table 6 are shown the effects of previous storage of Netted Gem tubers at 0° C. and at 5° C., on the subsequent gaseous exchange and production of blackheart when the tubers were placed in sealed chambers at 40° C., with a content of three volumes of air to one volume of tubers.

TABLE 6

THE EFFECT OF PREVIOUS STORAGE OF TUBERS AT 0° C. AND AT °5 C., ON THE GASEOUS EXCHANGE AND PRODUCTION OF BLACKHEART IN SEALED CHAMBERS AT 40° C.

	Time hours	2	3	4	5	6	7	8	9
Stored previously at 0°C.	CO_2 evolved %	2.0	3.6	5.2	8.0	6.8	11.2	12.2	.....
	O_2 remaining %	19.8	17.4	16.6	15.8	16.6	13.2	13.4	.....
	CO_2+O_2 present %	21.8	21.0	21.8	23.4	23.4	24.4	25.6	.....
	Tubers and blackheart.	8−	4− 2+ 1++	4+ 3++	4+ 2++ 2+++	3+ 3++ 2+++	3− 3+ 2++	1− 3+ 3++ 1+++	
Stored previously at 5° C.	CO_2 evolved %	.....	.....	2.8	3.4	6.0	4.8	.....	6.0
	O_2 remaining %	.....	.....	17.2	17.8	14.6	16.2	.....	15.4
	CO_2+O_2 present %.....	.....	.....	20.0	21.2	20.6	21.0	.....	21.4
	Tubers and blackheart.	.....	.....	8−	5− 5+	3− 5+	1− 4+ 4++	.....	2+ 4++ 1+++

DISCUSSION

1. THE BEHAVIOR OF DIFFERENT VARIETIES

At the highest temperatures no great difference appeared in the behavior of the three varieties of tubers used. In the experiments at 35° and 40° C., blackheart appeared at approximately the same time in each case. At these high temperatures the carbon dioxide evolved was relatively low and the oxygen residue in the jars relatively high in amount at the time when injury occurred. At 30°, 25° andd 20° C., marked divergence in behavior appeared. The Rural New Yorker and Green Mountain Jr. tubers were injured two or three days earlier than those of the Netted Gem variety. At these lower temperatures the

carbon dioxide production was relatively large and the oxygen residue relatively low at the time of injury. At 35° and 40° C., blackheart can be produced by heating tubers in normal air; at 30° C. this occurs infrequently and at 25° C. very rarely. Under the conditions of accelerated respiration in the heated tubers a slight reduction in the oxygen concentration of the surounding atmosphere decreased the rate of entrance of oxygen sufficiently to bring about its more rapid depletion in the tissues so that very early injury resulted. Owing to the rapidity of respiration at these higher temperatures differences in tubers of different varieties were largely obscured. At the lower temperatures of 20° to 30° C., the lower rate of respiration allowed the oxygen supply within the tissues to be maintained sufficiently high to delay injury until most of the oxygen had been removed from the atmosphere of the jars.

At 35° C., the consumption of oxygen in respiration appeared to be very nearly balanced with the rate of oxygen entrance. Injury produced by heating in normal air occurred only after several days exposure to this temperature and never appeared in all the tubers as at 40° C. A small reduction of oxygen concentration within the jars at 35° C. sufficed to retard oxygen entrance sufficiently to bring about deficiency of oxygen within the tissues, resulting in early injury. At 40° C. the rate of oxygen entrance was far from being equal to its rate of use, so that injury resulted still more quickly to tubers within the jars. At 30° C. heating in normal air infrequently results in injury and then only in a very few tubers and after long exposure. When the tubers were enclosed in jars at this temperature a much greater reduction of oxygen concentration, with correspondingly high concentration of carbon dioxide, occurred before depletion of oxygen in the tissues was sufficient to cause injury. This is still more evident in the experiments at 25° and 20° C. At the latter temperatures, Rural New Yorker and Green Mountain Jr. tubers reduced the oxygen concentration to 2.8 per cent and 1.0 per cent, respectively, before injury occurred, while Netted Gem tubers reduced it to zero.

The differences in the behavior of the different varieties are probably due in part to differences in permeability of the skin of the tubers to oxygen. Bartholomew found that removing the skin prevented or greatly delayed injury in tubers heated to 40° C. He also found[3] that surrounding the tubers with a high concentration of oxygen dur-

ing the period of heating prevented the injury. Both these results point to the skin as a highly important factor in the susceptibility of tubers to the development of blackheart. It is significant that Appleman[1] found the degree of suberization of the skin to have a marked effect upon the rate of respiration of potatoes. The existence of these marked differences in the permeability of the skins of tubers of different varieties does not appear to be generally recognized. Whether or not there are inherent differences in the activity of the protoplasm of different varieties appears to be unknown. There may be such differences, but it seems improbable that they had as much influence on the results of the present experiments as the permeability of the skin, since there was little difference in the behavior of the three varieties when inclosed in jars at high temperatures. The two factors, if both were present, cannot be distinguished with the available data.

2. The Exchange of Gases

It has been pointed out that at the higher temperatures the carbon dioxide content of the jars was relatively low and the oxygen content relatively high at the time blackheart appeared. This applies to the series at 45° and 40° C. for all varieties used and to Rural New Yorker and Green Mountain Jr. tubers at 35° C. At 35° C. the jars containing Netted Gem tubers showed a relatively high carbon dioxide and low oxygen concentration when blackheart appeared. At temperatures of 30° to 20° C., the carbon dioxide content of the jars was always relatively high and the oxygen content relatively low when blackheart occurred. In the series of jars at 30° to 20° C. containing Rural New Yorker and Green Mountain Jr. tubers, blackheart always occurred while a measurable amount of oxygen was still present in the jars, but where Netted Gem tubers were used blackheart did not appear in any case until the oxygen had been completely removed from the atmosphere of the jars. This brings out a marked difference in the behavior of the different varieties used. Bartholomew found that Rural New Yorker and Green Mountain Jr. tubers were readily injured by an exposure of 15 to 24 hours in normal air at 40° C. Netted Gem tubers, however, required an exposure of 24 to 48 hours under these conditions before injury occurred. This greater difficulty in producing injury in Netted Gem tubers was reflected in the results obtained when tubers were confined in jars. The lesser susceptibility of the Netted

Gem tubers allowed a greater accumulation of carbon dioxide and depletion of oxygen before the first appearance of blackheart in the series. This difference may have been due in a large measure to the greater permeability of the skins of Netted Gem tubers to oxygen.

As the temperature was lowered still further in the experiments with Netted Gem tubers a striking result appeared. At 30° C. and 25° C. injury appeared on the same day that the oxygen content of the jars fell to zero. At 20° C. injury was delayed until two days after complete removal of oxygen from the atmosphere of the jar. As the temperature was lowered still further this period of delay increased until at 5° C. the tubers were exposed to an atmosphere entirely devoid of oxygen for 42 days before injury appeared. With decrease of temperature below 5° C., the period without free oxygen necessary to produce injury decreased rapidly to 7 days at 0° C. This is shown in table 3, column 3. It seems remarkable that at any temperature living tissues of the type of potato tubers could withstand exposure to an oxygen-free atmosphere for 42 days before injury occurred. In all the series at different temperatures the tubers were in every way apparently normal and uninjured in every jar opened previous to the time of appearance of blackheart.

Some light may be thrown on these results by an examination of the data which show the absorption of oxygen and production of carbon dioxide (table 3, columns 4 and 5). It is evident from these values, in the range of temperature where oxygen was entirely removed from the atmosphere of the jars before blackheart occured, that the carbon dioxide produced was in nearly all cases equivalent to or slightly greater than the amount of oxygen originally present in the atmospheres of the jars, i.e., 21 per cent by volume. The oxygen rapidly absorbed in the early part of the experiment evidently served for the continuance of normal respiration after the oxygen had been completely removed from the surrounding atmosphere.

This table also brings out the fact that at all the temperatures, and especially at the lower temperatures, oxygen was absorbed much faster than carbon dioxide was produced. This difference caused a decrease in the sum of the oxygen and carbon dioxide present in the jars, the maximum decrease occurring later at the lower temperatures. Where the difference of rates was marked, a depression of the gas pressure occurred in the jars which in some cases was equivalent to a few centimeters of mercury.

It has long been known that the resipratory ratio frequently falls far below unity in plant tissues. Bonnier and Mangin[5] showed that with germination of starchy and proteinaceous seeds it was approximately unity for the first stages of germination and then fell below this value with increasing growth rates. Palladin[12] showed that rapidly growing internodes of various plants absorbed oxygen more rapidly than they produced carbon dioxide. The same investigators and others have shown that during the germination of fatty seeds the respiratory ratio is less than unity at first, gradually rising to near unity later. In all these cases very active tissues were used and the low value of the respiratory ratio was ascribed to the utilization of oxygen in the formation of substances requiring the addition of oxygen during synthesis. In mature, dormant or resting tissues the respiratory ratio at ordinary temperatures has commonly been found to be near unity except in the succulent plants which are noted for their accumulation of organic acids as a result of respiration (Puriewitsch;[13] Richards[14]). The minimum respiratory ratio was usually found to occur at 10° to 15° C. In the present experiments, before definite injury to the tubers occurred, the respiratory ratio was below unity though the whole range of temperature, and the greatest decrease from unity was found in the lower half of this range. Column 13, table 3, shows the values of CO_2/O_2 calculated from the results for the jars showing the lowest sum of carbon dioxide and oxygen in each series. The lowest value, 0.49, shows that during the first five weeks of the series at 7½° C., oxygen was absorbed on an average twice as rapidly as carbon dioxide was produced. Since this same phenomenon occurred in the early part of each series, it appears to be a normal occurrence with potato tubers and not a result of confinement in the jars. This point has not been studied under other experimental conditions.

In the light of the above data it appears probable that any supply of oxygen less than that necessary to maintain free oxygen in the atmosphere surrounding the tubers for one-half to all of their storage period in the range below ordinary room temperature, would be liable to result in blackheart. The amount of oxygen necessary to prevent the injury cannot be stated definitely but depends upon the temperature, the length of the storage period and the state of activity of the tubers, this depending upon the variety and the previous treatment. It appears highly improbable that such low oxygen concentration as is

required for the production of blackheart at low temperatures could ever develop in commercial cold-storage plants. It might possibly develop in unventilated storage pits. At higher temperatures it is obviously necessary to maintain a supply of air around the tubers sufficient to prevent the concentration of oxygen falling appreciably below that of normal air.

What the conditions may be which lead to the production of blackheart while the tubers are yet in the soil, are little known. Comparisons between tubers planted in jars of soil and tubers surrounded only by normal air, showed no significant differences. Temperature appeared to be the predominant factor. In the field, however, the conditions of aeration are probably quite different than in jars of soil, and the composition of the soil atmosphere may play a part. The high oxygen content known generally to exist in the upper layers of soil under good cultural conditions, indicates that temperature is the predominant factor. However, the high rate of oxygen absorption and carbon dioxide production by tubers at elevated temperatures, coupled with the limited volume of air in the soil and its slow diffusion through the soil, may quite possibly lead to a much different composition of the soil atmosphere in the region occupied by a hill of tubers, than in unoccupied regions. In addition, a high water content of the soil may be an important factor due to its relation to the air content. Some of the cases of blackheart reported from the field have been associated with early autumn rains coincident with moderately elevated temperatures.

3. The Rate of Respiration at Different Temperatures

In all cases a lowering of temperature in the range between 45° and 5° C., caused a decrease in the rate of respiration as indicated by carbon dioxide production. A lowering of 10° C. roughly halved the respiration rate, in agreement with the Van't Hoff-Arrhenius rule. There was large variation between the lots in different jars of the same series. This was probably due to variation among individual tubers and the use of a relatively small number of tubers in each jar. In producing blackheart by heating tubers to 38° to 40° C., it was found by Bartholomew that great variation existed in the response of individual tubers. Some showed severe, some slight and some no injury, when treated in exactly the same manner. While no evidence of varia-

tion in individual tubers was obtained by measurement of carbon dioxide production, it seems certain, from Bartholomew's observations and the results given in the present tables that such variation existed. It is unknown whether or not this variation was due to differences in the permeability of the skin to oxygen or to differences in the activity of the protoplasm.

In the range of 5° to 0° C., the effect of lowering the temperature was the reverse of that at higher temperatures. Tubers in jars at 0° C., were injured by one-half the period of exposure required to produce corresponding injury at 5° C. The actual periods were 37 days and 70 days for 0° and 5° C., respectively. At 2½° C., an exposure of 47 days was required to produce injury, and at 7½° C., an exposure of 50 days. The rate of respiration at the different temperatures was inversely proportional to the period required to produce injury. The respiration rate was markedly higher at 0° C. and at 2½° C., than at 5° C., and increased with temperature above 5° C.

There is indication in table 2, that the rate of respiration at 0° C. undergoes a marked change during the earlier part of the period of exposure. During the first week the carbon dioxide production was markedly lower at 0° than at 5° C. By the end of the first two weeks this difference had disappeared, and at the end of three weeks the tubers at 0° C., showed a larger total production of carbon dioxide than those at 5° C. The tubers used in the 0° C. series were stored at 5° C., previous to use in the experiment. When placed in the jars at 0° C., their immediate response was a slowing of the respiration rate, succeeded by a gradual acceleration of this rate until it exceeded that of tubers at 5° C. In two parallel series of jars at 0° C., containing tubers of the same variety and lot but with one containing tubers stored at 5° C., and the other at 0° C., for several weeks previous to use, the carbon dioxide production in the latter series was higher from the beginning than in the former. This is shown in table 4.

The observation that tubers show an increased rate of respiration at temperatures near 0° C., seems to have first been made by Müller-Thurgau.[10, 11] He held this to be due to the increased sugar content which occurs in potato tubers under such conditions of storage. The greatest accumulation of sugar was found by him to occur at 0° C. At higher temperatures the accumulation was less, the sugar content becoming normal at 6° to 10° C. The accumulation of sugar at 0° C.

was found to be gradual, reaching a maximum of 2 to 3.5 per cent of the fresh weight in two or three months. Different tubers showed great variation in the amount of sugars accumulated during equal periods, and in the maximum amount formed. At temperatures of 10° C., or higher, the normal content of sugar varied from none in new tubers to a maximum of about one-half of one per cent in old tubers.

The findings of Müller-Thurgau were confirmed by Boehm[4] and Butler,[6] and similar observations were made by Appleman.[2] These investigators appear to have carried out most of their measurements of respiration at room temperature. Müller-Thurgau, however, gives results for a comparison of sweet and non-sweet tubers at 0°, 10°, 20° and 25° C. At all these temperatures the sweet tubers, made so by previous storage at 0° C., showed a much higher rate of respiration than non-sweet tubers. Of most significance in relation to the present study, is the fact that in his experiments sweet tubers produced carbon dioxide about 40 per cent faster at 0° C., than did non-sweet tubers at 10° C. In the present experiments the respiration rate at 0° C. did not equal that at 10° C. The tubers used at 10° C., however, had been stored previous to use, at 5° C., at which temperature, according to Müller-Thurgau, some accumulation of sugar occurs. No determinations of sugar were made in the present study. However, the tubers in the jars at 0° C., removed after the second week, had a decidedly sweet taste.

None of the experiments of the investigators mentioned were carried out within the range of temperature between 0° and 10° C., and in all of them the respiration rate was measured over a relatively short period of a few hours to a few days. Ziegenbein's[16] measurements of the effect of temperature upon the rate of respiration of potato tubers were not carried below 10° C., except in one experiment at 0° C. for a very short period. The results of all these previous studies agree with those presented here for the corresponding temperature range.

The effect of exhaustion of free oxygen from the jars on the rate of carbon dioxide production is shown in table 4. In most cases this rate was reduced to one-half to two-thirds of its previous value with free oxygen present. The accumulated oxygen was apparently not as readily usable as free oxygen but sufficed to prevent the appearance of injury for an extended period at the lower temperatures. In this

table also, it appears that the respiration rate decreased till within the range of 5° to 7½° C., then showed no further decrease with decrease of temperature, but a distinct increase even with free oxygen absent. The values given are averages of the rates of all the jars at a given temperature removed during the two periods under comparison. To what extent, if any, the accumulation of carbon dioxide contributed toward the decrease in rate of respiration is unknown. The greatest change in rate occurred at about the time of exhaustion of free oxygen so that this appears to have had more effect than the gradual accumulation of carbon dioxide in the jars.

The existence of a minimum rate of respiration of potato tubers when stored at low temperatures for long periods, at approximately 5° C., does not appear to have been known previously. Measurements of respiration made over short periods, and when the tubers had very recently been placed at low temperatures would not show this. The existence of the minimum rate at 5° C., seems probably due to the occurrence at this point of an equilibrium between the opposing effects upon the respiration process of decreased temperature, and increased sugar content or factors correlated with it. This equilibrium point may vary somewhat with different varieties, and at different times in the life of the tubers. It probably varies also for different individual tubers of the same variety, for Müller-Thurgau found that the capacity to accumulate sugar varied with different tubers. Whether or not such a minimum point occurs in the respiration of other vegetable tissues is unknown. Müller-Thurgau[10] found that grape leaves, stalks of kohlrabi, and germinating hempseeds accumulated sugar when stored near 0° C. But no study appears to have been made of the respiration of these tissues.

4. Internal Conditions and Distribution of Injury in Tubers

In what form the excess of absorbed oxygen is held within the tuber is not known. Müller-Thurgau found an increase in the content of free malic acid in tubers placed at low temperatures, presumably the result of incomplete oxidation of certain substances within the tuber. This may, at least in part, account for the excess of oxygen absorbed by the tubers, as in the case of succulent plants. It seems possible also that the excess oxygen may become attached to some autoxidizable substance in the tuber as a peroxide which accumulates during the early

part of the life of the tuber and is utilized in the more rapid respiration occurring in later stages, when stored under normal conditions. In whatever form it occurred, it apparently was utilized by the tubers in the present experiments, since they showed a steady production of carbon dioxide without injury, although at a slower rate, for a considerable period after the exhaustion of free oxygen.

When the accumulated oxygen in the tubers disappeared, injury soon occurred. In table 3, column 15, is shown the carbon dioxide-oxygen ratio for the periods up to the time when blackheart appeared. In all cases, except one, it is close to or above unity. This indicates that as the tubers confined in a jar continued to respire, the free oxygen was absorbed and used until exhausted, then the oxygen accumulated in the tissues was utilized and the tissues maintained in apparently uninjured condition until the approximate equivalent of the oxygen originally available to the tubers had been converted into carbon dioxide. After this point had been reached the tissues were forced to respire anaerobically with injury rapidly resulting.

When blackheart was produced in tubers at higher temperatures, 20° C. and upward, whether in normal air or confined in jars, the injury was found to be entirely internal (plate 1), usually centrally located in the tubers. At temperatures below 20° C., in tubers confined in jars, the injury was usually both internal and on the surface of the tubers (plate 2). Surface injury often extended over one-half of the surface and into the tissues for several millimeters in severe cases, especially at the lower temperatures. Frequently, also, the injury appeared in very numerous small spots throughout the tuber (plate 3) giving an appearance resembling "frost necrosis" reported by Jones,[7] but not predominating in the region of the vascular ring. In such tubers the typical large irregular injured areas usually appeared as well as the surface injury. Surface injury was noted by Stewart and Mix in their experiments. The other type of injury, resembling "frost necrosis," was not mentioned by them, and may not have appeared in their experiments.

In the experiments reported here, surface injury never occurred, except in jars in which all the free oxygen had been exhausted, for sometime before its appearance. Under these conditions the accumulated oxygen apparently became well distributed and was used up about equally in all parts of the tuber. Injury then occurred at any

point in the tuber where oxygen deficiency occurred. At the higher temperatures, however, the appearance of injury coincident with or before the exhaustion of free oxygen indicated that uniform distribution of either free or accumulated oxygen did not occur, and injury resulted rapidly in those tissues farthest removed from the source of supply. It is possible also that the accumulated oxygen in the tissues is not normally equally distributed throughout the tuber, but is largely held in the outer tissues, making these much less liable to injury by oxygen depletion. Oxidase action was found to be most marked in the outer tissues as indicated by the direct blueing of guaiacum tincture, which is dependent upon the presence in the tissues of a substance equivalent to hydrogen peroxide in its relation to the reaction involved. The tissues immediately outside the vascular ring were always the last to succumb at low temperatures.

The presence of surface injury when tubers were injured at low temperatures through exhaustion of oxygen was so generally present as to constitute an indication of the conditions under which injury had occurred. On the other hand, the appearance of internal injury alone in large areas indicated that the injury had occurred at high temperatures with little or no depletion of oxygen in the atmosphere surrounding the tubers. This is in complete agreement with the statements of Stewart and Mix.[15]

The accumulation of carbon dioxide in the jars appeared to have no relation to the injury. When excessively high concentrations of carbon dioxide occurred, in some cases 30 per cent or over, the tubers usually were flabby and exuded water, resembling tubers which had been frozen and thawed. Blackheart was always severe in such cases but had usually appeared earlier in the series. It is presumed that the carbon dioxide concentration within the tissues was always as high as, and probably higher at all times, than in the surrounding atmosphere. This was found to be the case by Magness[8] in his study of the composition of the gases in the intercellular spaces of apples and potatoes. With both of these, increase of temperature increased the proportion of carbon dioxide to oxygen in the tissues. The low amount of oxygen found by Magness in the tissues exposed at the higher temperatures lends support to the belief that anaerobic conditions develop within the tissues before blackheart occurs.

The accumulation of sugar in tubers, induced by long exposure to low temperatures, apparently made them somewhat more susceptible to injury when heated at 40° C. in normal air. Tables 5 and 6 show the results of such experiments. The increased rate of respiration found associated with increased sugar content by Müller-Thurgau, and shown to occur at higher as well as lower temperatures, would be expected to hasten the approach of conditions in the tuber which would result in its injury. This appeared to be the case, since for equal periods of exposure to 40° C., in normal air, more tubers were injured in the early stages in the lot previously held at 0° C., than in that held at 5° C. In the later stages injury was also much more severe in the former lot. When lots of the same tubers were sealed in jars the same results appeared and the gaseous exchange agreed with that previously described for tubers stored in sealed jars for long periods at 0° and 5° C. It may be safely stated that tubers which have been subjected to low temperatures sufficiently long to cause them to accumulate sugar in their tissues are more liable to develop blackheart than normal tubers when subjected either to high temperature, or to low temperature and depleted oxygen supply.

SUMMARY

1. A definite relation between temperature, oxygen supply, and period of exposure required to produce blackheart, has been shown.

2. Differences in the readiness with which the different varieties used could be injured by heating at high temperatures in normal air were largely eliminated when the tubers were heated while confined in jars with six volumes of air to one volume of tubers.

3. When tubers were confined in jars and heated to temperatures of 20° to 30° C., which are too low to cause injury with the tubers surrounded by normal air, differences in behavior appeared which corresponded to the differences exhibited by the different varieties when heated in normal air at 35° to 40° C. Netted Gem tubers at 20° to 30° C. required a longer period of heating than the other two varieties to produce injury, and this did not occur until the free oxygen content of the jars had been entirely exhausted. Rural New Yorker and Green Mountain Jr. tubers were injured more quickly and always before the disappearance of the free oxygen in the jar.

4. Differences in the behavior of the different varieties at high temperatures may be due to differences in the permeability of the skins to oxygen. All the evidence points toward the permeability of the skin as an important factor affecting the rate of respiration of potato tubers.

5. As the temperature was lowered, longer periods of confinement in the jars were necessary to produce injury, until 5° C. was passed. At temperatures of 2.5° C. and 0° C., injury occurred more quickly than at 5° C.

6. Lowering the temperature caused a decrease in the rate of respiration as indicated by the carbon dioxide output, in accordance with the Van't Hoff-Arrhenius rule, between 45° C., and 5° C. Decreasing the temperature below 5° C. caused an increase in the rate of respiration. The rate of respiration at 0° C. was nearly as high as at 10° C. The existence of a minimum rate of respiration at 5° C. appears to be the result of an equilibrium between the decreasing effect of a lower temperature, and the increasing effect of an increased sugar content on the respiration process as shown by other investigations.

7. In all cases, oxygen was absorbed more rapidly than carbon dioxide was produced during the early part of the experiments, and the respiratory ratio at the lower temperatures was less than at the higher temperatures.

8. At low temperatures injury to tubers did not occur until a considerable period had elapsed after the exhaustion of the oxygen from the atmosphere of the jar. The maximum period of exposure to an atmosphere devoid of oxygen before injury occurred was 42 days at 5° C.

9. Injury did not occur at the lower temperatures until the approximate equivalent of the available free oxygen had been returned as carbon dioxide to the atmosphere of the jar.

10. The rate of respiration before exhaustion of free oxygen was about twice as great as afterwards. The tubers apparently used the oxygen accumulated in the tissues, but with more difficulty than the free oxygen from the surrounding atmosphere.

11. The actual injury evidently resulted when anaerobic conditions were brought about in the tissues, and may be attributed to processes initiated as a result of those conditions.

12. Tubers confined at 20° C., or higher, invariably showed only typical internal blackheart as described originally by Bartholomew. Tubers injured at 15° C., or below, usually showed both internal and surface injury, and occasionally a diffuse injury throughout the tissues.

13. The accumulation of carbon dioxide in the jars appeared to have no close relation to the production of blackheart.

14. Tubers exposed to low temperatures until they became sweet appeared to be more easily injured by high temperatures than non-sweet tubers.

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PLATE 1

Typical blackheart produced by high temperature. No injury appears on the surface of the tubers.

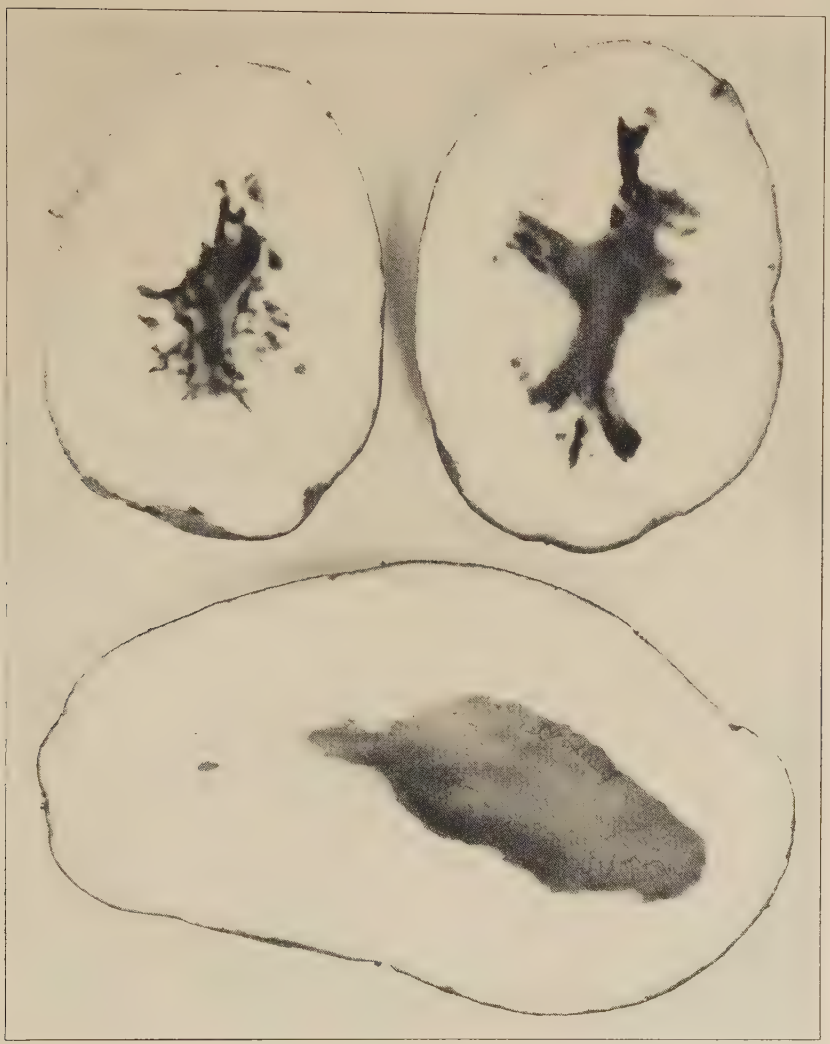

PLATE 2

Severe blackheart produced at low temperature (2½° C.) with deficiency of oxygen in sealed container. Severe injury appears in interior and on surface of tubers.

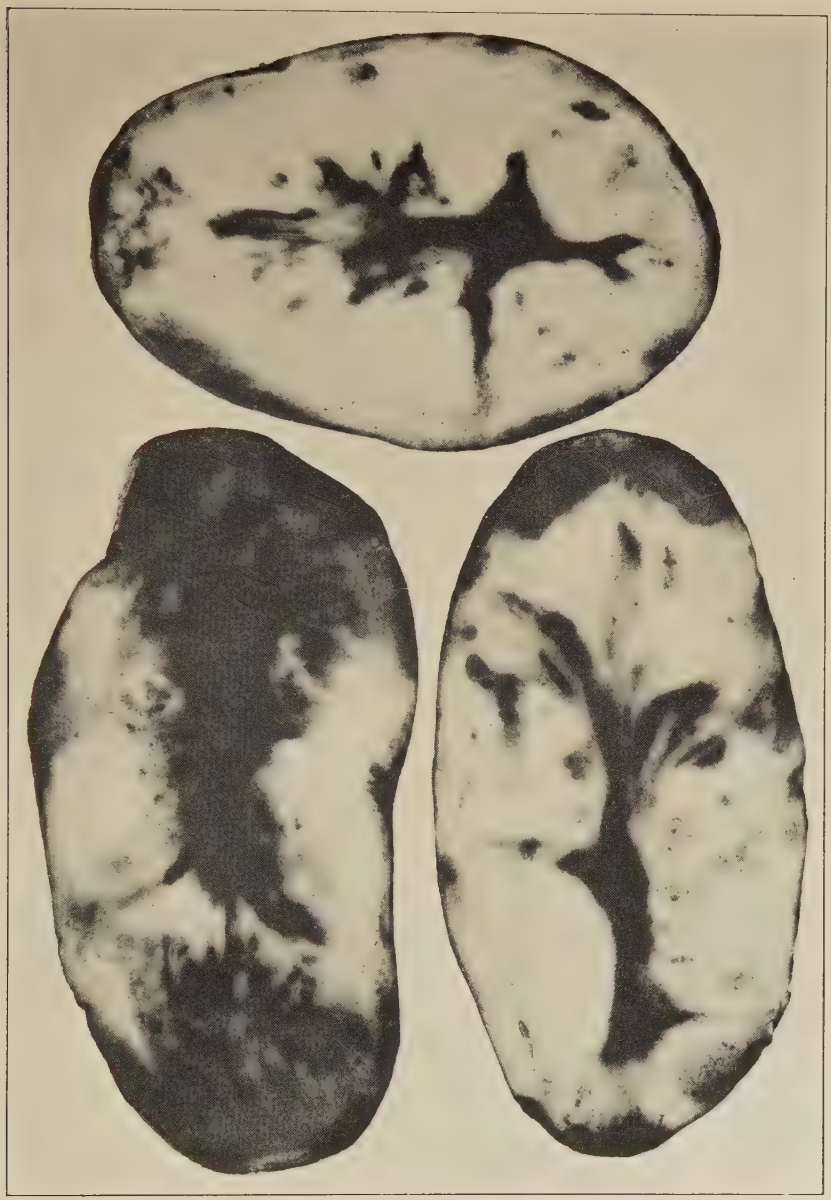

PLATE 3

Diffuse type of injury occurring occasionally in tubers kept in sealed containers at low temperatures.